Behavior of Animals that ROCK this World (2007) 23:829-846

Pit building and Location Strategies of the Antlion *Myrmeleon immaculatus*.

Sophia R. Roberts
Department of Biology, University of Michigan Biological Station, Pellston, Michigan

Abstract

Antlion larvae *Myrmeleon immaculatus* are sit-and-wait predators, that construct pits in the sand. The quality of the pit greatly affects the foraging success. Antlions face the trade-off between a high quality pit and reserving energy stores. In this study we examined the effects of feeding frequency, substrate size, temperature and location on pit size. Antlions and sand were collected from Pine Point on Douglas Lake and from Sturgeon Bay. We found that antlions will abandon pits to better capture success if not sufficiently fed. In Sturgeon Bay antlions build larger pits than Douglas Lake antlions. There was no effect of substrate or angle of repose leading us to think the difference is due to higher temperatures in Sturgeon Bay.

Introduction

Antlions build pit traps to capture mobile prey by means of the sit-and-wait strategy. Antlions are best recognized and defined by their distinctive larval form. By lingering hidden at the bottom of their pits, antlions prey on passing ants. Antlions will often move from presumably undesirable locations, leaving a clear path giving them the common name "doodle bug." Research suggests many reasons for this particular behavior of antlions. We collected antlions and the sand they inhabit from Sturgeon Bay and Pine Point on Douglas Lake to compare. In this study, we explored the conditions that induce travel, the creation of a new pit, the size of the pit, the location of the pit as well as the correlations of antlion size to pit.

Distance

As sit-and-wait predators, antlions rely on the location of their pits for survival. An antlion has little to no success capturing prey without a pit. An antlion located in sand too shallow to build a pit is predicted to move. In this study, we will determine if such conditions compel the antlion to move.

Feeding Frequency and Pit Construction in Antlions: High vs. Low Feeding Frequency

Antlions move for many reasons. The marginal value theory suggests that a forager attempts to maximize energy intake per unit time. Antlions should leave a location if the net gain is average or falls below the environmental average (Scharf and Ovadia 2005). Availability of prey coupled with the size of the antlion are the primary determinants of pit relocation and size. Prey-rich antlions have been recorded to experience higher rates of mortality in relocation due to their higher metabolic rates, in comparison to antlions from prey-poor locations. (Scharf and Ovadia 2005). In addition to moving less frequently, prey-rich antlions move shorter distances than prey-poor antlions and compensate for less movement by slowly enlarging the pit over several days (Heinrich and Heinrich, 1984). Medium sized antlions are reported most likely to move in a starvation experiment, with the reasoning that large antlions are usually less hungry

and have higher tolerances to heat (Scharf and Ovadia 2005). In addition to relocations, prey availability influences the size of the pit. Arnett and Gotelli (2001) demonstrated that low-food treatments maintained pit depth and quality. Prey is more profitable to poorly fed antlions so they are compelled to maintain well-structured pits. Antlions that remain to be unfed long enough will not enlarge their pits but frequently move as a means of sampling the different locations (Heinrich and Heinrich, 1984).

In addition to feeding frequency, disturbance plays a concern in the size of the pit. Disturbed antlions build smaller pits than undisturbed antlions . Antlions that are hungry build pits faster than prey satiated antlions (Scharf and Ovadia 2005).

The marginal value theory does not incorporate non-foraging factors, such as environmental factors. Crowley and Linton (1999) suggest that antlions track sources of shade depending on the average soil temperature. The paper also mentions that in the field treatment, antlions moved only every few weeks rather to the every several days in the lab treatment

In this study we predict several factors to influence the probability an antlion will construct a new pit. The high feeding frequency antlions are predicted to remain in their original pit as well as have less maintained, shallower pits. The low frequency feeding antlions are predicted to have some relocations and higher quality pits. We also predict low frequency antlions to build their pits faster than the high frequency antlions when the pits are disturbed.

Effect of Substrate on Pit Size: Sturgeon Bay vs. South Fish Tail Bay

Does substrate particle size affect pit building decision? An antlion's livelihood depends on the quality of the pit it creates. The trap should enhance capture efficiency and antlions should design pits in such a way as to maximize the probability of capturing their prey (Devetak *et al.* 2005). This study also found that the largest pits were built using sand particle size of .23-.54mm and could not build pit with grains larger than 1mm in size.

The combination of an increasing angle size with decreasing particle size produced pits with the best capture rate (Devetak *et al*. 2005). Further research indicates that smaller grains stick better to the walls of the pit from low drag-to-momentum ratio. (Allen and Croft, 1985) In considering the effect of substrate, we must account for the size of the antlion. Increasing weight may decrease the efficiency of the pit despite there being a correlation between pit size and antlion size. Prior observations suggest that Pits made in Sturgeon Bay (SB) are larger. Based on these observations, we predict SB to have smaller gain diameters than Douglas Lake (DL) sand. This assumption also predicts that DL pits to have pits with shallower angles of repose. To test this we plan to measure antlion pits from both locations in the wild as well as in the lab. The lab portion will test whether pit sizes are repeatable, as we hypothesize. The antlions will also be compared in their sand of origin as well as in the other location's sand (Kiddy pool). We will also investigate the differences in angles of repose. We predicted SB to have larger pits and subsequently hypothesize SB to have a steeper angle of repose to match.

Half-pipe Array

Some spiders, scorpions and insects identify and locate prey by vibratory signals. Recent research suggests that antlions detect their prey by sensing the vibrations that prey generate while moving. The property of the sand, grain size, determines the length the signals can travel; greater grain sizes conduct higher frequencies for the antlion to detect (Devetak *et al.*, 2007). In our study, we plan to determine how antlions assess a location by mean of environmental cues. Three treatments, no ants, foraging ants and alarmed ants will be presented to antlions. We

predict antlions in the foraging and alarm treatments to either not move or move towards the ants. By detecting the ants' presence nearby, they are predicted to remain relatively stationary and attempt to build a pit. Antlions in the control treatment that lack ants are predicted to move more than the other treatments because they cannot detect ants and want to find them. We plan to observe the antlions in the array three times a day, to test an effect of time of day. Were the animals more mobile during hot times of day? This is not the same question as did their pit-building depend on temperature but it is related. Both have to do with amount of activity and temperature

.

Methods and Materials

Distance

To measure the distance an antlion will travel, we constructed an unsuitable environment. We filled a 3.5x2ft board with approximately 1.5in of filtered and sterilized sand. The depth of the sand was deep enough for the antlion to submerge itself, but too shallow to build a pit. The "doodle board" should essentially be considered a large rock the antlion will want to move away from. The antlions chosen ranged greatly in size and were left on the "doodle board" for approximately a week. The antlions chosen for the doodle board were collected from East South Fishtail Bay on Douglas Lake, Pellston, Michigan .The antlions had received fairly regular feedings up until a few days before being placed on the board. Pipes 1-3 test the effect of the alarm pheromone, 3-4 ants are trapped in the tubes. Pipes 4-6

Feeding Frequency and Pit Construction in Ant Lions

We collected and weighed 60 specimen of *Myrmeleon imaculata* from East South Fishtail Bay of Douglas Lake. All the antlions were placed in plastic cups (11.5 cm in diameter) in about 5 cm deep 1mm sifted sand. The 60 antlions were randomly segregated into 2 equal treatments, a high and low feeding frequency. The low frequency group (LFG) was fed one antlion the morning after collection, at approximately 8:15 am, most antlions had built pits. The high frequency group (HFG) was fed one ant three times a day for ten days at 7:30, 11:30 and 18:00. For the first two days the antlions were fed smaller ants that were hypothesized to be toxic, therefore all antlions were subsequently fed larger ants from that point. During the morning feedings, the pits were checked over for additional doodles or pits. After ten days of feeding the antlion pits were smoothed over, the antlion was removed from the pit, and the container shaken to re-level the sand. The subsequent time to complete pit construction was measured along with the final pit diameter, depth. Pit diameter was determined by dropping a piece of spaghetti over the pit's center and measuring with calibrators the distance where the spaghetti first touches the sand. The depth, was determined by lowering a piece of spaghetti vertically into the pit. The point where the vertical piece of spaghetti hit the horizontal piece of spaghetti was marked and measured.

Effect of Substrate on Pit Size, Pit Construction in Relation to Soil Type: Sturgeon Bay vs. South Fish Tail Bay

We compared the sizes of Sturgeon Bay and Douglas Lake pits both in the field and in the lab. We measured the diameters and depths of the pits without collecting the antlions in both locations as well as collecting antlions to be used in controlled lab settings. A sample of 40 antlions was collected from Sturgeon Bay. All were placed in plastic cups (11.5 cm in diameter)

in about 5 cm deep sifted sand. Two treatments were created, one with Sturgeon Bay sand (N = 20), the other Douglas Lake sand (N = 20). Each ant lion was fed one ant per day for 4 days in order to minimize differences in hunger. After a period of 5 days the pits were measured, the diameter and height. The next day, all the antlions were switched to sand of the other location. The antlions were removed from the sand and transferred to the other type of sand (trial 2), which was leveled and stirred to homogenize any potential scent of the previous antlion. The antlions were given one additional day to build a pit in the new sand and the pits were once again measured. Due to the decreased heat in the building and the night, an infrared heat lamp was placed above the two treatments. We used ANCOVAs to determine differences. Trial 1 had SB animals in either SB or DL sand, indoors, temp around 21 C.

Artificial Pits

To determine the angle of repose for each type of sand we artificially created pits. We stacked three circular plastic tubs that were 5 cm deep and 11 cm across so that the bottoms of the to two met in the middle and the bottom two met at the opening. The top two cups had pin holes in the centers so a small steady stream of sand could flow through the first two into the third. A perfect cone was formed when the stream stopped. To prevent avalanches, we sprayed the pits with "Herbal Essences" hairspray. The diameters and depths of both SB and DL sand five times to ensure consistency.

Kiddy Pools

We filled two kiddy pools with SB sand and another two with DL sand. Each combination of pools were then filled with SB antlions and the other with DL antlions. The pools were 30 cm deep, 150 cm across and were located on a Douglas Lake beachfront. By placing this combination of antlions together, we can determine if the differences in pits are due to a difference in antlions or in the environments.

Half-pipe Array

We constructed an array to measure the choice direction an antlion will travel under three conditions. An anthill was surrounded with 20ft long black garden edge with the inside covered with tanglefoot. The tanglefoot prevents the ants from traveling over the edge and thus are directed towards the array. The array is a 4.5x3ft board bordered on three sides with 5in. aluminum flashing. Inside are 9 1.5in inner diameter PVC pipes cut in half, filled with .75 mL of sand. At the centers of each pipe are dividers the ants cannot pass but the antlions can. Pipes 1-3 test the effect of the ant alarm pheromone. 4-5 ants were trapped in the pipes; the antlion had the option of moving towards or away from the ant area of the pipe. Pipes 4-6 provide free movement for both the ants and antlion. A weigh boat filled with tissue paper soaked in sugar water is placed in the center of the pipe where the ants can forage. Pipes 7-9 have no ants and acts as a control. Antlions were first placed 3cm from the center divide rotated 90˚, that is perpendicular from the openings of the pipes on the ant-free end of the pipe. Actions were recorded for 45 minutes. The antlions were removed at that time and placed 3cm from the divide on the side the ants have access. The antlions' actions were again recorded for another 45 minutes. By observing the antlions during three parts of the day we are studying the behavioral character

Results

Distance

This aspect of the study just observed whether the antlions would move. Neither length nor direction were recorded. All antlions placed on the doodle board moved.

Feeding Frequency and Pit Construction in Ant Lions: high vs. low feeding frequency

We used a Chi-square test to see if the low frequency acted as expected. This is a goodness of fit test for a 2x2 design. Only the low frequency antlions made second pits. The test was significant, $\chi^2 = 6.8$, and critical value was 3.84 at 1 df. Time also reported insignificant for differences between the two treatments. ($Z = -0.848$, $p = 0.396$). The same values from the extra pit formation were calculated for antlions that doodled (moved locations).

Effect of Substrate on Pit Size: Sturgeon Bay vs. South Fish Tail Bay

An analysis of covariance (ANCOVA) revealed an effect of mass and adjusted for that to expose the effect of location on pit diameter. SB antlions report heavier than DL antlions ($F_{1,112} = 68.77$, $P < 10^{-6}$). SB antlions also report building larger pits than DL antlions, revealing the site effect ($F_{3,112} = 8.49$, $P = 4 * 10^{-5}$). Slopes comparing mass to diameter width for both SB and DL antlions were homogenous, indicating that there is no between site and mass but merely an effect of site (group*mass interaction, $F_{3,112} = 2.12$, $P = 0.10$). Conclusions inferred about mass and effect are reported in confidence due to the relatively high $R^2 = 0.72$, indicating that 72% of all the variance is explained. *(See Figure 1).*

A Tukey HSD *Post hoc* test described the explicit differences in diameters between the groups, again illustrating that SB pits are wider. SB pits during the month of July reported larger than DL pits (df = 112, P = 0.00014). SB pits were larger than DL pits in August as well (df = 112, P = 0.00014). SB pits were consistent in width across time, resulting in no significant difference between the months (df = 112, P = 1.00). DL pits were similarly constant in width over time (df = 112, P = 0.91).

We found a site and mass effect comparing pit depths between July and August, with mass as a covariate by analyzing the covariance. The mass effect indicates that mass influences the depth of the pit ($F_{1,112} = 28.71$, $P < 10^{-6}$). Adjusting for mass revealed the group effect. SB pits report deeper than DL pits ($F_{3,112} = 9.33$, $P = 1.5 * 10^{-5}$). No interaction between mass and depth were found, meaning the slopes were homogenous (group*mass interaction, $F_{3,112} = 1.37$, $P = 0.26$). *(See Figure 2)*

Post hoc tests further illustrated the differences between the two sites. SB pits reported deeper than DL pits in July (df = 112, P = 0.00014). SB pits were also deeper than DL pits in August (df = 112, P = 0.00014). There was an unexpected effect of time in SB depths, where pits measure in August were deeper than in July (df = 112, P = 0.00017). DL pits were consistent in depth over time (df = 112, P = 0.91).

Artificial Pits

A difference in pit size could be due to a difference in grain size. Sturgeon Bay has a higher percentage of smaller grains than Douglas Lake sand. *(See Figure 3).*

Creating the artificial pits served to compare the behaviors of the sand types. The angles of repose reported steeper in the DL sand than the SB sand, where the median angle or repose for DL sand = 39.4157, $CI_{95} \pm 6.68$. The median angle of repose for SB was 40.2163, $CI_{95} \pm 2.9$. we

found mp difference in angles between the two types of sand (SB N = 10, DL N = 9, U = 38.00000, Z = 0.571548, P = 0.567629).

Common garden kiddy pool

An ANCOVA testing diameter and mass established that there was no effect of group, unlike findings from the wild ($F_{3,100} = 0.66$, P = 0.58). There was an effect of mass ($F_{1,100} = 5.98$, P = 0.016). Very little of the variance is explain using these data, as is indicated by the $R^2 = 0.13$. The slopes were homogenous (group*mass interaction, $F_{3,100} = 0.44$, P = 0.73). No *post hoc* tests were completed due to the lack of a group effect. *(See figure 3).*

An ANCOVA testing the depth and mass found no group effect ($F_{3,100} = 0.37$, P = 0.78). There was an effect of mass ($F_{1,100} = 4.19$, P = 0.04). The slopes reported homogenous (group*mass interaction, $F_{3,100} = 0.86$, P = 0.47). Conclusions based upon these data are tentative; the adjusted $R^2 = 0.031$. In other words, only 3.1% of the variance is explained. *(See Figure 4).*

Alternative explanations, abiotic or biotic, for the site difference in the wild and not in the study were explored. Temperature loggers indicate the larger pits could be an effect of heat. Sturgeon Bay temperatures peaked an average, over 5° C higher each day than Douglas Lake. *(See Figure 5).*

Trial 1 vs Trial 2:

The ANCOVA comparing diameter to mass found neither an effect of mass nor a group effect. The groups reported no effect of group, SB or DL sand ($F_{3,66} = 1.19$, P = 0.32). Surprisingly there was not effect of mass ($F_{1,66} = 1.26$, P = 0.27). We will treat these results similarily to the others because the $R^2 = 0.24$. The slopes reported homogenous (group*mass interaction, $F_{3,66} = 0.78$, P = 0.50). *(See Figure 6).*

The ANCOVA comparing pit depths to mass also found no significant results. We found no effect of mass ($F_{1,66} = 0.28$, P = 0.60). We report not group effects ($F_{1,66} = 0.28$, P = 0.60). The adjusted $R^2 = 0.11$, and attributes very little of the variance to the variables presented. The slopes reported homogenous (group*mass interaction, $F_{3,66} = 0.58$, P = 0.63). *(See Figure 7).*

Sturgeon Bay antlions made pits in both Sturgeon Bay sand and Douglas Lake sand. Comparing the diameters in a paired test between trials 1 and 2 yielded of group A unexpected results. The diameters reported larger in the Douglas Lake sand (trial 2) than in the Sturgeon Bay sand (trial 1), ($M_{trial\ 1} = 52.47$ SD = 7.419, $M_{trial\ 2} = 63.86$ SD = 12.12, t = -3.663, df = 16, p = 0.002). Similarly, in another paired t-test, depth reported greater in the Douglas Lake sand than in the Sturgeon Bay sand ($M_{trial\ 1} = 20.46$ SD = 2.87, $M_{trial\ 2} = 22.70$ SD = 3.21, t = -3.576, df = 16, p = 0.003). Comparing group B between the trials reverted results back to their expected values. Antlions in SB sand (trial 2) produced pits with diameters larger than antlions in DL sand (trial 1) ($M_{trial\ 1} = 52.46$ SD = 9.09, $M_{trial\ 2} = 63.89$, t = -4.334, df = 16, p = .001). Antlions in SB sand (trial 2) also recorded greater depths than when in the DL sand (trial 1) (M_{trial} 1= 21.04 SD = 3.87, $M_{trial\ 2} = 23.77$ SD = 1.91, t = -2.860, df = 16, p = .011).

Half-Pipe Array

Data concerning the Array failed the test for normality (the distances traveled), so a non-parametric Kruskal-Wallis ANOVA was conducted. We compared 4 days of array data, and found there was a main effect of time of day Kruskal-Wallis test: H (2, N= 216) =31.35075 p <

0.0001). Antlions moved more with duration of day, the longest distances were made in the evening and the shortest during the morning. *(See Figure 8).*

Discussion

Distance

This portion of the study served as a preliminary observation to determine whether the antlions would move. Without the advantage of a pit, antlions have very little chance of capturing prey (Heinrich and Heinrich 1983). The conditions were not conducive to building pits. Moving suggests antlions actively seek an area with suitable provisions. Although each individual antlion was left on the doodle board for the duration of about a week, they did not move very far. We did not record exact measurements, but no antlion surpassed a distance of one foot before stopping to remain in the same location. Antlions must allocate energy moving similarly to building a pit, where metabolic activity increases ten-fold. Energy inputs may not be quite so large during movement but it certainly limits the distance an antlion is willing or can move in any one given week.

Feeding Frequency

We found that the availability of food to influenced the probability an antlion will abandon its pit for a new one. The marginal value theorem predicts this very effect. Over the course of ten days, 30% of the low feeding frequency antlions moved. Antlions will often wait months without food. Does the quick decision to move indicate previous feeding frequencies were higher? We unfortunately had no means of measuring conditions prior to our study, but such information would provide more definitive conclusions. Research also indicated a difference in reconstruction time, but this was not supported by our data. The direct effects of a difference in feeding over ten days was also not measured. Substantial inferences can only be made considering the difference in mass and final masses were not taken. By measuring the weights, we could infer the store of lipids. Fat stores dictate the necessity of food and subsequently moving. Large energetic costs are paid by antlions in building pits because increased prey capture enhances fat stores (Arnett and Gotelli 2000). We suspect antlions that moved had lower fat stores.

Effect of Substrate size, in the wild

We observed a difference in pit size according to location between Sturgeon Bay and Pine Point on Douglas Lake. SB pits were both wider and deeper than DL pits. What biotic or abiotic factors clarify such differences between two regions? Antlions face a trade-off by investing energy to acquire food. Antlions are capable of waiting long periods of time without eating and reduced maintenance costs will enable the predator to withstand long periods of starvation (Lucas 1985). To explain the differences between these two locations, we compared the effects of grain sizes and temperature.

Sand particle size greatly influences that efficiency of a pit. Research suggests antlions can discriminate particle sizes when selecting a site location (PAPER). There is a trade-off between the grain sizes. Larger grains can are thrown further, but smaller grains cling to the edges of the pit more than larger particles, making escape harder for prey (Allen and Croft 1885). Smaller grains are also easier to manipulate, especially for smaller antlions, quickening the pit building process (Devetak *et al.* 2005).

The quality of the ant population should affect antlion activity. The size of the available ants could influence pit sizes. Larger ants were more likely to fall and roll uncontrollably than smaller ants. Ants also have decreasing escape probabilities with decreasing grain size (Devetak *et al.* 2005). A steady diet of large ants could explain the difference. The quantity of ants in the antlion habitats naturally impacted pit sizes. Trap design influences trade-off between benefits of prey and reduced maintenance costs. If a reduction in metabolism decreases the ability to catch prey, more efficient traps will offset this cost and allow for a reduction in maintenance costs (Lucas 1985).

Low temperature are found to reduce pit-building (Arnett and Gotelli 2000). The temperature loggers revealed vast temperature difference between Sturgeon Bay and Douglas Lake of about 5° C. Pits along Douglas Lake are surrounded by vegetation and trees unlike open dunes of Sturgeon Bay. At the same point each day, the Douglas Lake region experiences shade, which greatly decreases the sand temperature and metabolic rates of the antlions. This conclusion, however contradicts the conclusions of Lucas. He suggests that antlions occupying shaded regions have comparatively higher metabolic rates (at least in later instars) than sun-adapted species (Lucas1985). This conclusion assumes that, given the same conditions, antlions originating from shaded regions should devote similar amounts of energy because they internally up-regulate metabolic efforts that the sun manages for sun adapted antlions. We tested this very consideration in the common garden experiment.

Artificial pits

We found that Sturgeon Bay had a greater percentage of smaller grain sizes, which is consistent with the notion that smaller grain diameters allow for larger pit sizes. There was no difference in the angles of repose when producing artificial pits, suggesting that the differences in the grains were not great enough to impact the angles. Artificial pits lack the off-centering that antlion made pits include. The off-centering decreases the architectural efficiency. Antlions compensate for this by engaging in attack behavior by flicking sand at the ant attempting to escape (Fertin and Casas 2006). The SB antlions don't seem to be counteracting compromised pit angles with increased diameter, something else must influence the differences in location.

Kiddy pool (30 cm or 3 decameter deep, 150 cm)

If differences in the sand are responsible for the differences in the pit dimensions, then putting the two sand types in the same place under the same conditions should not affect the difference between populations in pit dimensions. The "common garden" experiment controlled for differences of conditions by placing them in the same location and from that we can infer that we have no support for a substrate difference. What could account for the differences, are they internal or external? Do we think that the population difference has a genetic component? Great fault lies in the methodology. More conclusive results could be made if another set of antlions were placed in Sturgeon Bay. The differences would also be controlled for. Because the pits in the kiddy pools were measured by different people than the pits in the wild, the effect of disturbance cannot be assessed. Although Day and Zalucki (2000) suggest there is no trend to suggest that daily disturbance of antlions influences pit size.

Trial 1 vs trial 2

This study was originally designed to investigate the effects of substrate like the kiddy pool experiment. We found the IR heat lamp produced a confounding effect of heat and

redirected our observations to consider those effects. We raised the temperature of trial 2, which yielded support for the temperature effect. This further supports reasons why SB pits were larger than DL pits.

The flawed methods negatively affected our results. We found no effect of mass, which was regularly found in the measurements made in the wild. The low temperatures in the lab spoiled the design to test the characteristics of the sand. We have little confidence in the results reported by the ANCOVA. What the experiment revealed was the influences of temperature on pit size. Activity is reduced at low temperatures (Arnett and Gotelli 2000). We concluded from the kiddy pool experiment that substrate size does not influence pit size, and temperature may be a reason behind it. The ANVOCA did not reveals an effect of group but looking at the paired tests, which are more sensitive statistical tests, comparing trials 1 and 2 within groups A and B better illustrates the differences the heat created.

HPA

This study was originally created to test the effects ant activity had on the physical position of the antlion. Nothing conclusive was determined due to poor planning in methodology and data entry. In regards to the aspect of distance traveled towards or away from the ants we suggest future study. Little research incorporates the element of ants, the primary focus of antlions.

This arrangement revealed an effect of time where antlions are most active during the evening. This further confirms the effect of heat increasing metabolic rates. In order to conserve energy, and maintain fat stores, antlions should best operate later in the day. Research found antlions to restrict their activity to the cooler parts of the day and were more abundant in the shade than in sunny areas (Van Zyl *et al*. 1996). Fat stores also depend on the age of the larva, antlions in the third instar have higher fat stores and are subsequently able to afford longer waits in between eating and higher temperatures (Griffths 1991).

Summary

In this comprehensive examination of antlions we found several defining influences on antlion behavior. Antlions will move to better capture success, if not sufficiently fed. Sturgeon Bay has larger pits than Douglas Lake. The most definitive reason for the difference is due to heat. We found substrate to have no effect, nor the angle of repose.

Literature cited

Allen, G.R. and Croft, D.B. 1985. Soil Particle size and pit Morphology of the Australian Ant-Lions Myrmeleon diminutus and M. pictifrons (Neuroptera : Myrmeleontidae). Austrialian Journal of Zoology 33: 863-74.

Arnett, A. E., and Gotelli, N. J., 2001. Pit-Building Decisions of Larval Ant Lions: Effects of Larval Age, Temperature, Food and Population Source. Journal of Insect Behavior 14:1 89-97.

Crowley, P. H., Linton, M. 1999. Antlion Foraging: Tacking prey across space and time. Ecology 80(7) 2271-2282.

Day, M. D. and Zalucki, M. P. (2000). Effect of density on spatial distribution, pit formation and

pit diameter of *Myrmeleon acer* Walker, (Neuroptera: Myrmeleontidae): patterns and processes. Austral Ecology 25:1 58–64.

Detvetak, D. *et al*. 2007. Sand as a medium for transmission of vibratory signals of prey in antlions *Euro nostras* (Neuroptera: Myrmeleontidae). Physiological Entomology

Devetak, D. , Spernjak, A. , and Janzekovic, F. 2005. Substrate particle size affects pit building decision and pit size in the antlion larvae *Euroleon nostras* (Neuroptera: Myrmeleontidae). Physiological Entomology 30: 158-163.

Eltz, T. 1997. Foraging in the ant-lion Myrmeleon mobilis Hagen 1888 (Neuroptera: Myrmeleontidae): Behavioral flexibility of a sit-and-wait predator. Journal of Insect Behavior 10:1 1-12.

Fertin, A. and Casas, J. (2006). Efficiency of antlion construction. Journal of Experimental Biology 209: 3510-3515.

Griffiths, D. (1991). Food Availability and the Use and Storage of Fat by Ant-Lion Larvae. Oikos 60:2 162-172.

Heinrich, B., Heinrich. M. 1984. The pit-trapping strategy of the antlion, *Myrmeleon immaculatus* DeGeer (Neuroptera: Myrmeleontidae). Behavioral Ecology and Sociobiology 14:151-160.

Lucas, J.R. (1985). Metabolic Rates and Pit-Construction Costs of Two Antlion Species. The Journal of Animal Ecology 54:1 295-309.

Scharf, I. , and Ovadia, O. 2006. Factors Influencing Site Abandonment and Site Selection in a Sit-and-Wait Predator: A Review of Pit Building Antlion Larvae. Journal of Insect Behavior 19:2 197-217.

Van Zyl, A ,Van der Linde, T.C.K. and Van der Westhuizen, M.C. (1996). Ecological aspects of pitbuilding and non-pitbuilding antlions (Neuroptera: Myrmeleontidae) in the Kalahari. African Entomology 4:2 143-152.

Figure Legends

1. Pit Diameters at Sturgeon Bay and Pine Point, 2007

2. Pit Depths at Sturgeon Bay and Pine Point, 2007

3. Sand fraction size distribution

4. Pit Diameters in “Common Garden”, 2007

5. Pit Depths in “Common Garden”, 2007

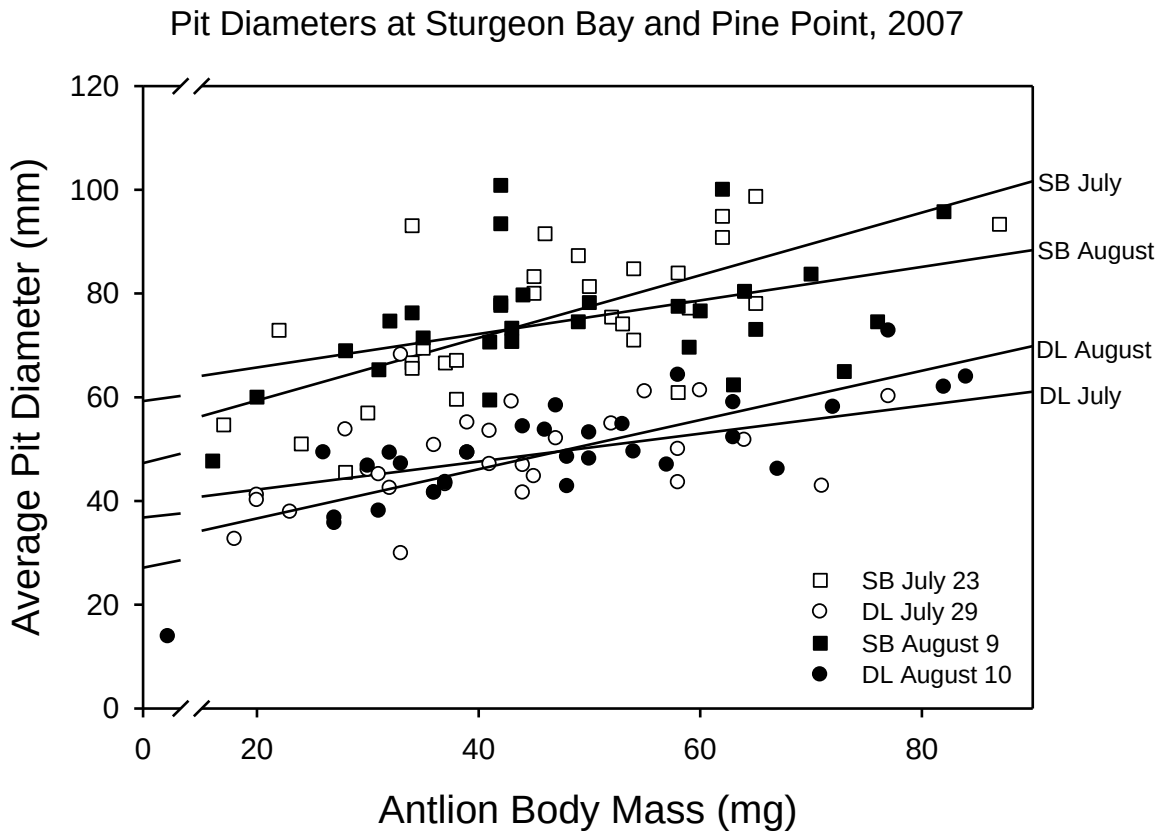
6. Surface Temperature At Sturgeon Bay and Pine Pt, 2007

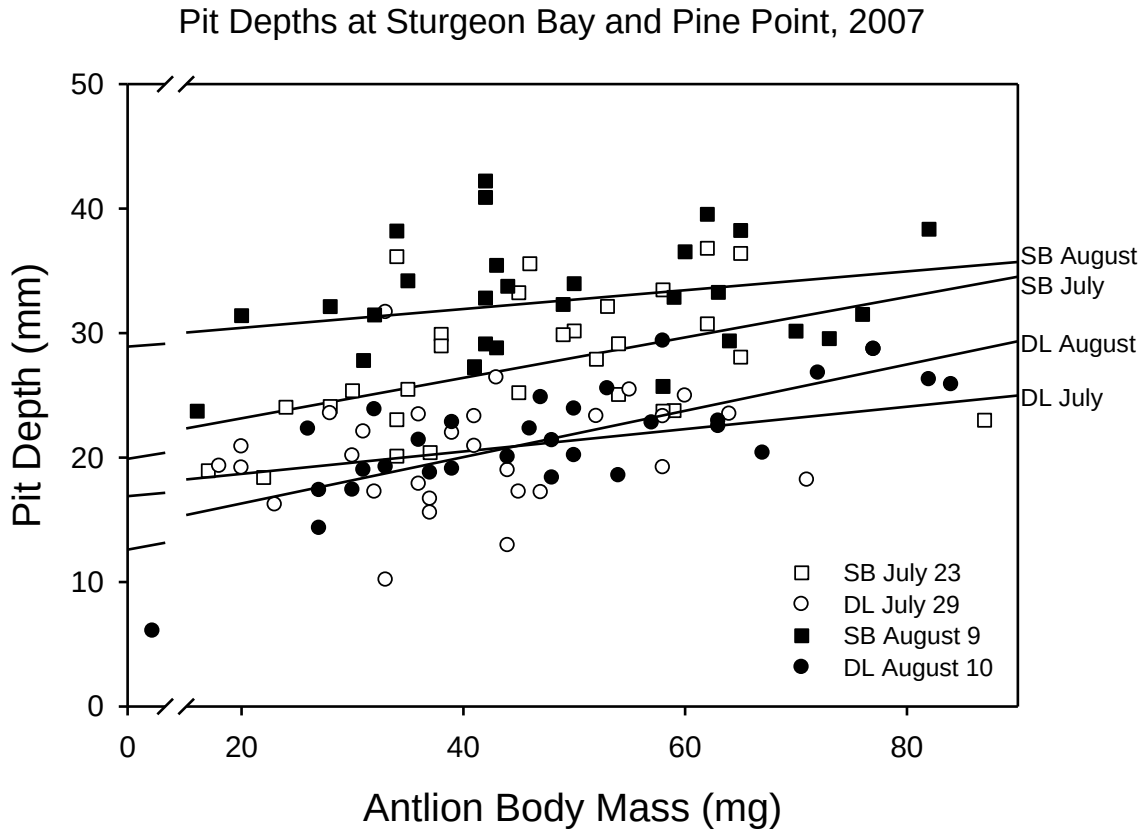
7. Pit Diameter in Lab, 2007

8. Pit Depth in Lab 2007

9. Distance Moved in Half-Pipe Array

Behavior of Animals that ROCK this World (2007) 23:829-846





Figures 1 and 2

Behavior of Animals that ROCK this World (2007) 23:829-846

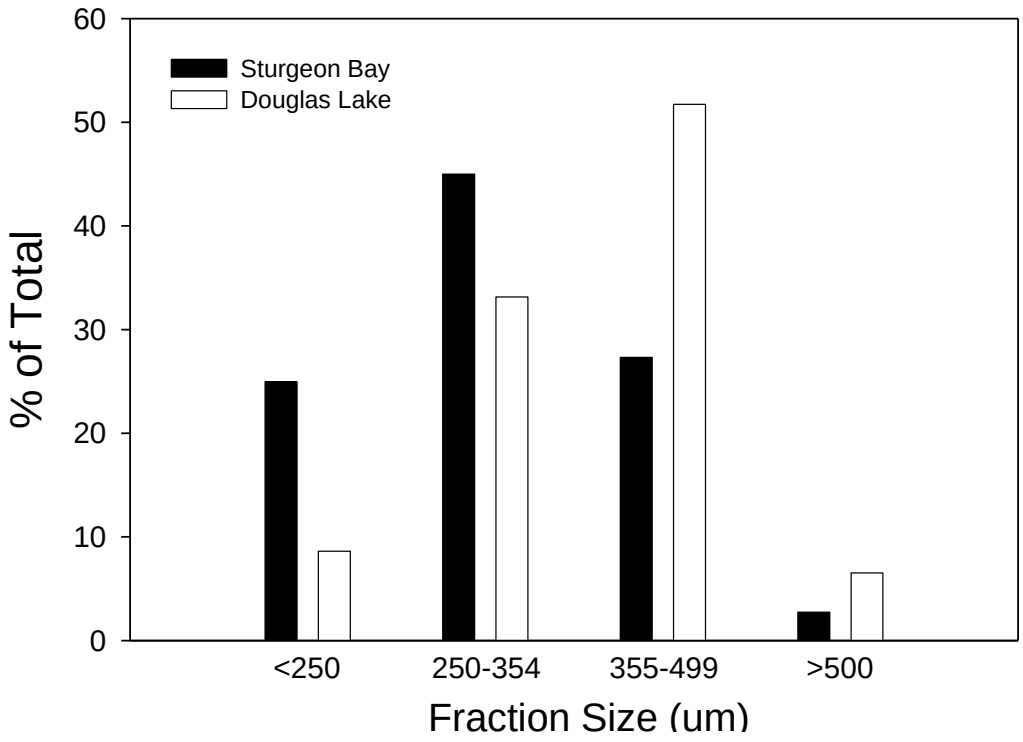
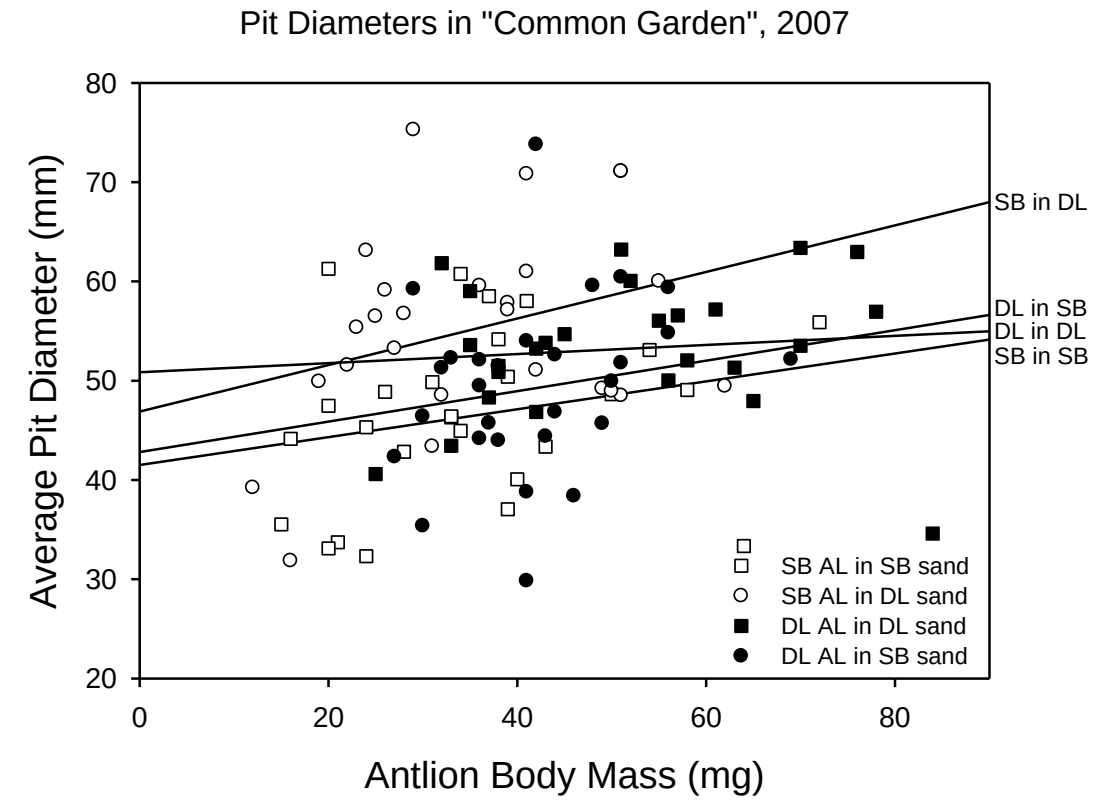
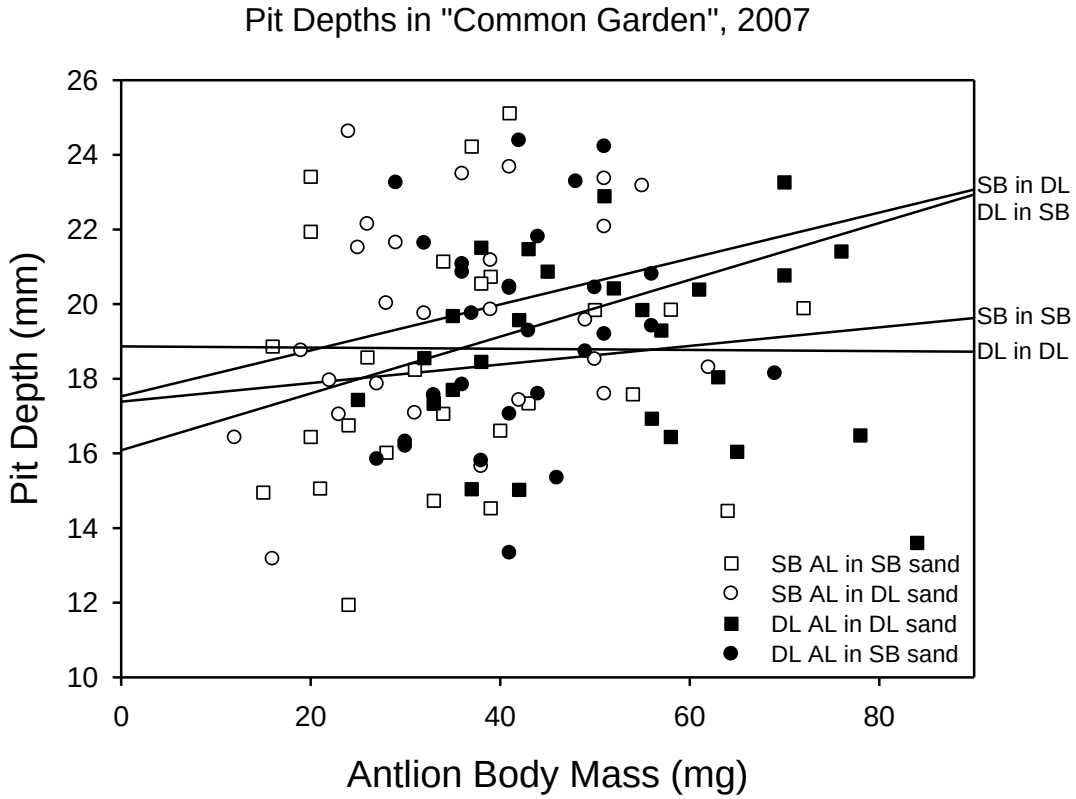


Figure 3

Behavior of Animals that ROCK this World (2007) 23:829-846





Figures 4 and 5

Behavior of Animals that ROCK this World (2007) 23:829-846

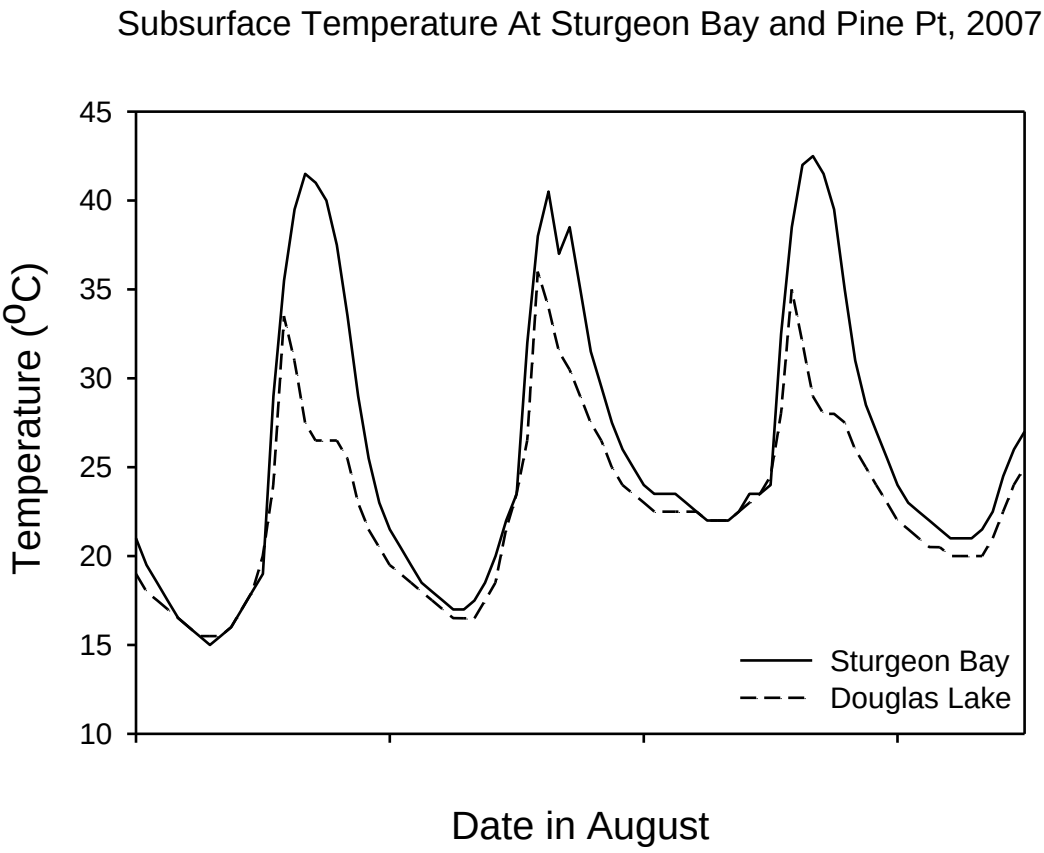
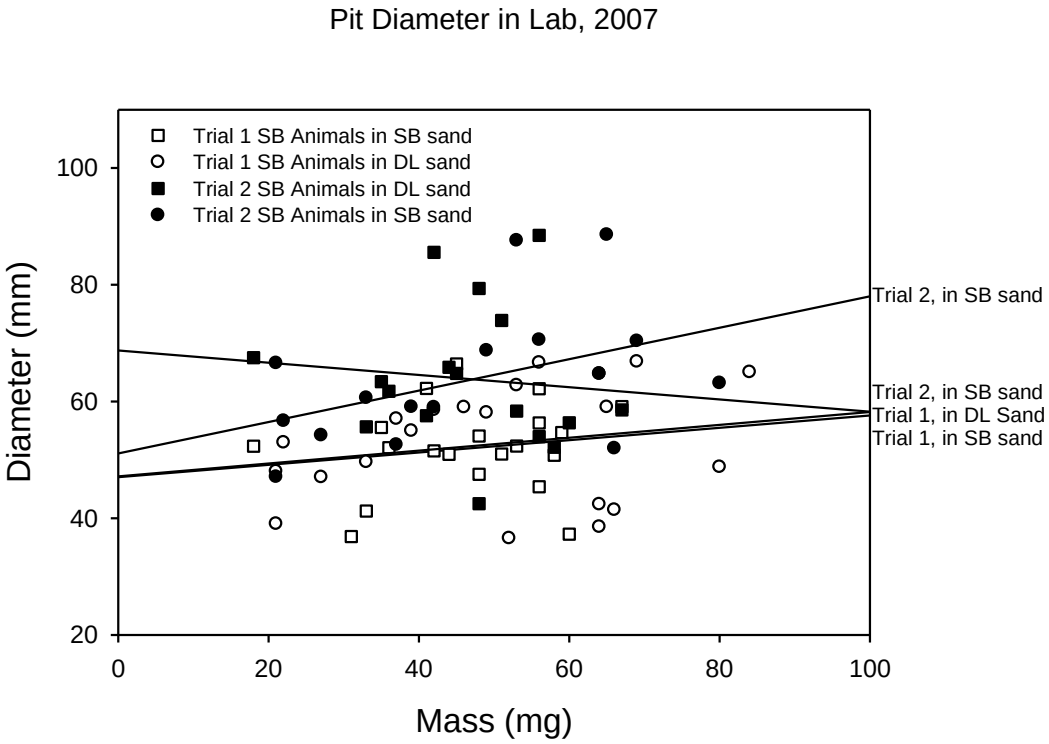
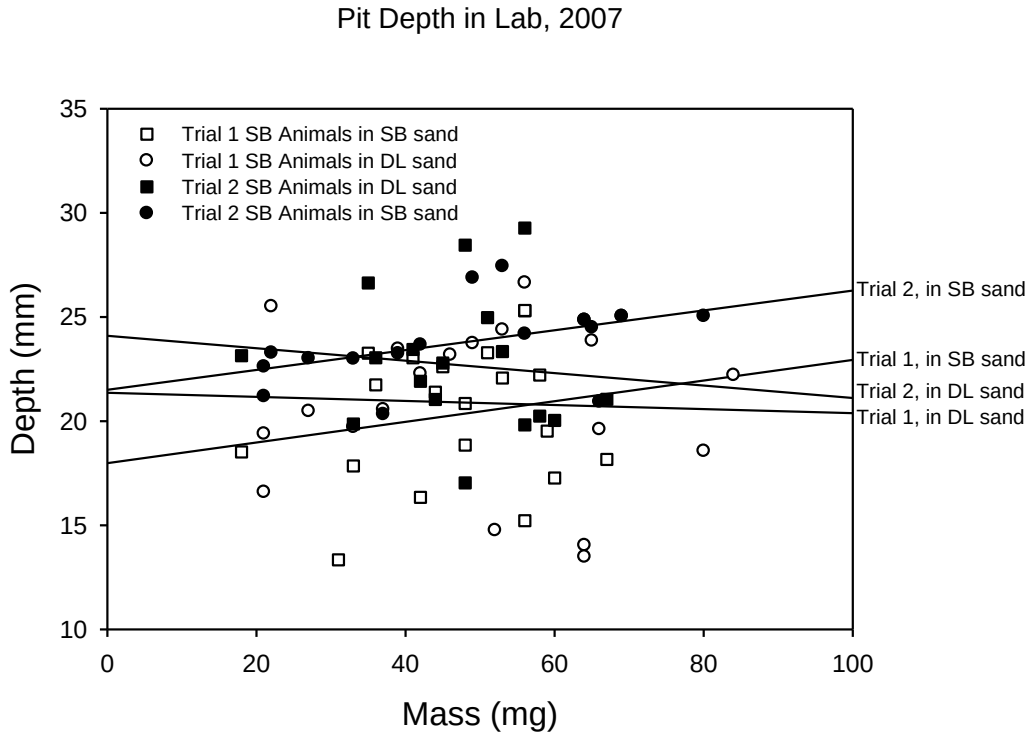


Figure 6

Behavior of Animals that ROCK this World (2007) 23:829-846





Figures 7and 8

Behavior of Animals that ROCK this World (2007) 23:829-846

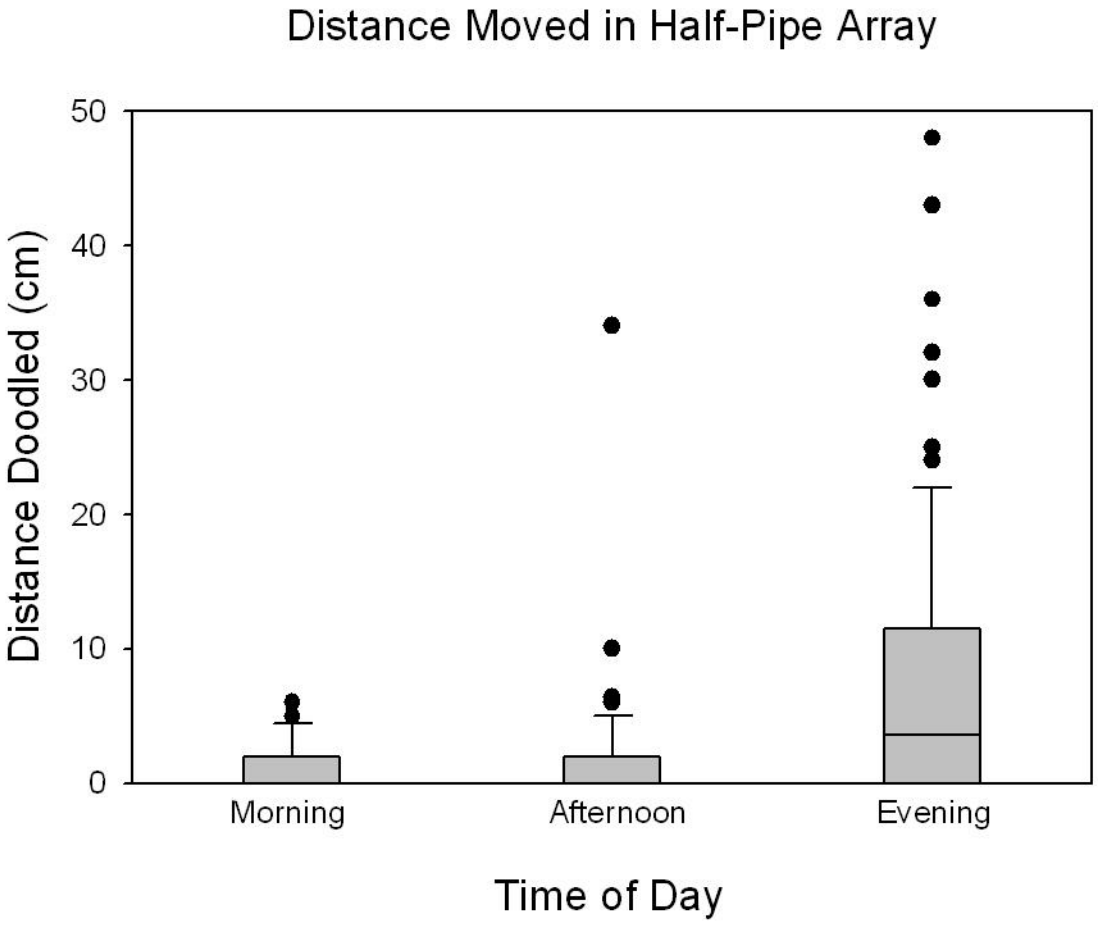


Figure 9